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A new species of *Schizopygopsis* Steindachner, 1866 (Cypriniformes, Cyprinidae) from the Yalong River on the Qinghai-Tibetan Plateau, China

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Abstract

Schizopygopsis malacanthus Herzenstein, 1891, a fish species native to the Qinghai-Tibetan Plateau, is widely distributed upstream of the Jinsha and Yalong Rivers. Comprehensive analyses were conducted on all geographic populations of *S. malacanthus* and the coexisting fish *Herzensteinia microcephalus* (Herzenstein, 1891). Morphological examination revealed that the Yalong River population of *S. malacanthus* can be distinguished from other *Schizopygopsis* species according to its phenotypic characteristics, including the origin of the ventral fin under the 4th–5th branched ray of the dorsal fin, strong unbranched rays of the dorsal fins, hooked pharyngeal bones, and shovel-shaped or oblique-truncated grinding surfaces of the pharyngeal teeth. The phylogenetic and genetic analyses revealed monophyly of the Yalong River population of *S. malacanthus*, with genetic distances ranging from 2.03—6.16% from those of other *Schizopygopsis* species. Consistent with the molecular evidence, species delimitation clearly revealed that the Yalong River population of *S. malacanthus* is distinct from other *Schizopygopsis* populations. Therefore, we present *Schizopygopsis yalongensis* **sp. nov.** as a valid species through integrative taxonomy, resolving the taxonomic ambiguity of the *Schizopygopsis* fishes in the Yalong River. These results increase known fish diversity and highlight cryptic species present in the river system of the Qinghai-Tibetan Plateau.

Key Words

Cyt *b* gene, new species, phylogeny, *Schizopygopsis yalongensis*, taxonomy

Introduction

The genus *Schizopygopsis* (Cypriniformes, Cyprinidae, Schizothoracinae) was described by Steindachner in 1866 and includes a group of fish species that are widely distributed in the lakes and rivers of the Qinghai-Tibetan Plateau (QTP) (Wu and Wu 1992). *Schizopygopsis* species are highly specialized Schizothoracine fishes with characteristics including nearly no scales, no barbels, inferior or subinferior mouths, lower jaws with sharp horny layers, and sparse gill rakers (Nichols and Chu 1935; Wu and Wu 1992; Chen and Cao 2000). Based on the morphological variations in the number of gill rakers, the origin of the ventral fin, and the ray of the dorsal fin, Chen and Cao (2000) identified 12 species and subspecies in the genus *Schizopygopsis*, whereas 9 species were defined by Wu and Wu (1992). The major difference between these two studies is the taxonomic statuses of four species: *Schizopygopsis chengi* Fang, 1936, *Schizopygopsis anteroventris* Wu & Tsao, 1989 and *Schizopygopsis microcephalus* Herzenstein, 1891 are delineated as independent species in the genus *Schizopygopsis* by Wu and Wu (1992), whereas Chen and Cao (2000) define *Schizopygopsis kessleri* Herzenstein, 1891 as valid

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species and *Herzensteinia microcephalus* (Herzenstein, 1891) in the monomorphic genus *Herzensteinia*.

Schizopygopsis malacanthus was described by Herzenstein in 1891, with the type locality in the Tongtian River, the headwater of the Jinsha River (Cao and Deng 1962; Wu and Wu 1992). It includes two subspecies: *Schizopygopsis malacanthus malacanthus* Herzenstein, 1981 in the upper and middle streams of the Yalong and Jinsha Rivers (the Chumar River, Tuotuo River, Dang Qu, and Tongtian River) and *Schizopygopsis malacanthus chengi* (Fang), 1936 in the upstream of the Dadu River (Cao and Deng 1962; Chen and Cao 2000). On the basis of genetic, phylogenetic, and morphological evidence, recent studies have revised the taxonomic status of *S. chengi* as a valid species in its own right, and the speciation process might be related to geographic isolation between the Jinsha and Dadu Rivers (Yu et al. 2006; Qi et al. 2015; Tian et al. 2025). For *S. malacanthus* from the Yalong and Jinsha Rivers, previous studies have revealed their genetic divergences and differences in the numbers of inner and outer gill rakers (Wu and Wu 1992; Li et al. 2020; Wang et al. 2022). However, the lack of comprehensive molecular data and morphological comparisons of *Schizopygopsis* fish led to the classification of *S. malacanthus* from Yalong as a geographic population or evolutionarily significant unit (ESU) rather than an independent species.

To confirm the taxonomic position of the Yalong River population of *S. malacanthus*, we compared it with all 10 *Schizopygopsis* fish species, including the populations of *S. malacanthus* in the Jinsha River Basin, *Schizopygopsis kialingensis* W. X. Tsao & C. L. Tun, 1962, *Schizopygopsis pylzovil* Kessler, 1876, *S. kessleri*, *S. chengi*, *S. anteroventris*, *Schizopygopsis younghusbandi* Regan, 1905, *Schizopygopsis thermalis* Herzenstein, 1891, *Schizopygopsis stoliczkai* Steindachner, 1866 and *H. microcephalus*. *Herzensteinia microcephalus* was included in the present study for two reasons. First, *H. microcephalus* was defined as *Schizopygopsis microcephalus* by Wu and Wu (1992). Second, several studies have revealed that the lineage of *H. microcephalus* is nested within *Schizopygopsis* fishes in phylogenetic trees (He and Chen 2007; Qi et al. 2015; Tian et al. 2025). The genetic and morphological characteristics of the specimens of *S. malacanthus* and *H. microcephalus* from the Yalong and Jinsha Rivers were carefully examined to clarify the taxonomic status of *S. malacanthus* in the Yalong River.

Materials and methods

Sampling and ethics statement

Fish samples were collected from upstream regions of the Jinsha River and its largest tributary, the Yalong River, from 2021–2023. In total, 41 and 20 specimens were collected from populations of *S. malacanthus* from the Yalong River and Jinsha River, respectively. Additionally, 29 samples of *H. microcephalus* were collected upstream of the Jinsha River, including the Chumar River, Tuotuo River, Dang Qu River, and Tongtian River (Fig. 1 and Table 1). These

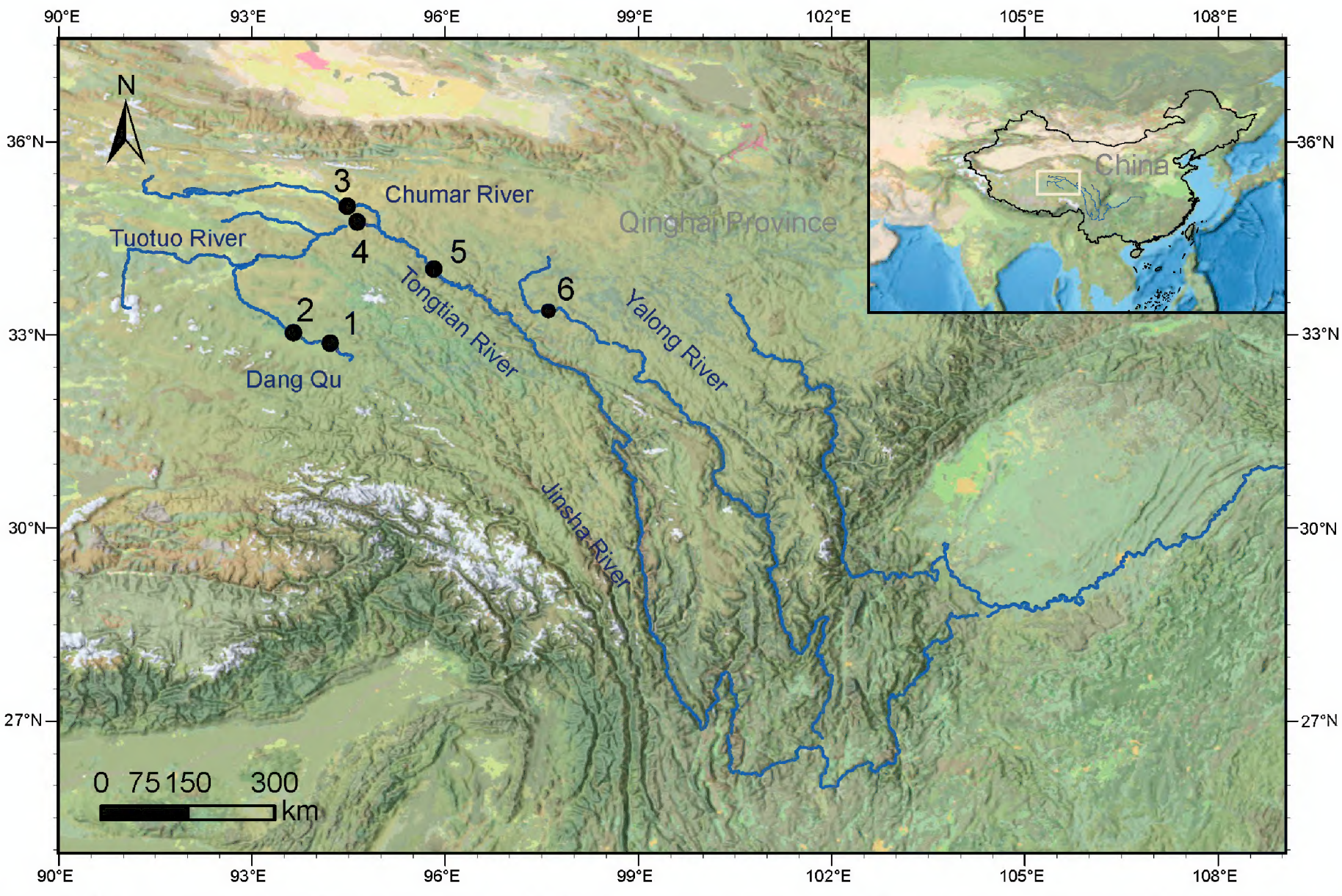

Figure 1. Sampling localities. The white square indicates the sampling area. 1–5 indicate the sampling sites in the Jinsha River (1 and 2 in the Dang Qu River, 3 in the Chumar River, 4 in the Tuotuo River, and 5 in the Tongtian River), and 6 denotes the sampling site in the Yalong River. For information on sampling locations refer to Table 1.

Table 1. Sampling information.

Species	Sampling locality	Basin	Sampling sites	Number of samples
S. yalongensis	Yalong River,	Yalong River	6	41
S. malacanthus	Tongtian River	Jinsha River	5	20
H. microcephalus	Tongtian River,	Jinsha River	5	6
	Dang Qu River,	Jinsha River	1–2	10
	Chumaer River	Jinsha River	3	4
	Tuotuo River	Jinsha River	4	9

samples were subjected to both morphological and molecular analyses. The samples were collected using a seine net and then euthanized with 200 mg/L MS222 (Sigma, USA), then preserved in 95% ethanol for morphological and molecular analyses. All samples were voucher labelled and deposited at the Northwest Institute of Plateau Biology at the Chinese Academy of Sciences. The field surveys were permitted and supervised by the Qinghai Provincial Bureau of Fishery. The sampling procedures were performed in accordance with the guidelines described in the "Guidelines for Animal Care and Use" manual approved by the Animal Care and Use Committee, Northwest Institute of Plateau Biology, Chinese Academy of Sciences.

Morphological analysis

Herzensteinia microcephalus and *S. malacanthus* were identified on the basis of descriptions from Chen and Cao (2000) and Wu and Wu (1992). Seventeen morphological characteristics, including total length (L_t), standard length (L_s), body height (BH), head length (HL), caudal peduncle length (CPL), caudal peduncle depth (CPD), predorsal length (PDL), prepectoral length (PPL), preventral length (PEL), preanal length (PAL), head depth (HD), head width (HW), eye diameter (ED), interorbital width (IEW), snout length (SL), mouth width (MW), and postorbital length (PL) were measured on the right side of all samples using digital callipers. We then calculated the ratios of BH, HL, CPL, CPD, PDL, PPL, PEL and PAL to L_S and the ratios of HD, HW, ED, IEW, SL, MW and PL to HL; the ratio of CPD to CPL; the ratio of MW to SL; and the ratio of IEW to ED. The ratios of measurements from all individuals were applied for principal component analysis (PCA) in R (v 4.3.2, 2023). Additionally, the first gill arch was collected from the right side of specimens and the numbers of inner and outer gill rakers (ING and ONG) were counted. A microCT system (Quantum GX 3.1.4, Perkinelmer, USA) was used to scan and record the number of vertebrae from the samples, with the following parameters: scan model = high resolution, scan time = 4 min, FOV = 86 mm, voltage = 90 kV and X–ray filter = Cu 0.06 +Al 0.5.

We also examined the specimens of 10 congeners in the genus *Schizopygopsis*, including *S. kialingensis*, *S. pylzovi*, *S. chengi*, *S. malacanthus*, *S. younghusbandi*, *S. thermalis*, *S. stoliczkai*, *S. kessleri*, *S. anteroventris*, and *H. microcephalus*, which were obtained from the Qinghai-Tibet Biological Specimen Museum, Northwest Institute of Plateau Biology, Chinese Academy of Sciences (Table 2).

Comparative material

Specimens of *Schizopygopsis* fishes were obtained from the Qinghai-Tibetan Plateau Biota Museum at the Northwest Institute of Plateau Biology, Chinese Academy of Sciences, Xining, Qinghai Province.

Table 2. Information of specimens analyzed in the study.

Specimens	Voucher number	Sampling location	Basin	Cyt *b* (Genbank No)	Source
S. yalongensis	NWIPB2307001– NWIPB2307041	Yalong River,	Yalong River	PV872040–PV872057	This study
S. malacanthus	NWIPB2206043– NWIPB2206062	Tongtian River,	Yangtze River	PV916945–PV916949	This study
H. microcephalus	NWIPB2306001–NWIPB2306006	Tongtian River,	Yangtze River	PV916950–PV916960, PV929440–PV929443 PX658883–PX658890	This study
	NWIPB2306007–NWIPB2306016	Dangqu River,	Yangtze River		
	NWIPB2306017–NWIPB2306020	Chumaer River	Yangtze River		
	NWIPB2306021–NWIPB2307029	Tuotuo River	Yangtze River		
S. chengi	NWIPB2107011, NWIPB2107012	Marke River	Dadu River	OR972943, OR972944	GenBank
S. kessleri	NWIBP2007051, NWIBP2007054	Golmud River	Qaidam Basin	MN267668, MN267669	GenBank
S. pylzovi	NWIPB1205412–5	Yellow River	Yellow River	KY461363, KY461364	GenBank
S. stoliczkai	NWIPB1007024, NWIPB100705	Qaraqash River	Hotan River	KY461356, KY461357	GenBank
	NWIPB1160487	Pangong Co	Pangong Co		GenBank
	NWIPB1160383	Lake Manasarovar	Lake Manasarovar		GenBank
S. thermalis	NWIPB1170189–NWIPB1170192	Yuqu River	Nu Jiang	KY461318, KY461319	GenBank
S. younghusbandi	NWIBP1160962–3	Pengqu River	Ganges River	KY461322, KY461323	GenBank
	NWIPB0906028–9	Nyang River	Yarlung Zangbo River		GenBank
S. kialingensis	NWIPB1108004–007	Bailong River	Jialing River	KY461338–KY461340	GenBank
S. anteroventris	NWIPB1108432–5	Lancang River	Lancang River	KY461341–KY461343	GenBank
O. stewartii	T78	Yarlung Zangbo River	Yarlung Zangbo River	KY461387	GenBank
G. pachycheilus	T621	Yellow River	Yellow River	KY461377	GenBank
G. dybowskii	1007174	Kaidu River	Tarim River	KJ081379	GenBank
D.maculatus	1305134	Ili River	Ili River	KX022699	GenBank
G. integrigymnatus	T1530	Longchuan Jiang	Jinsha Jiang	KY461321	GenBank

Schizopygopsis yalongensis: NWIPB2307001–NWIPB2307041, 41 specimens, 65.0–196.0 mm SL, the Yalong River, Chenduo County, Qinghai Province.

Schizopygopsis malacanthus: NWIPB2206043–NWIPB2206062, 20 specimens, 69.0–252.4 mm SL, the Tongtian River, Zhiduo County, Qinghai Province.

Herzensteinia microcephalus: NWIPB2306001–NWIPB2306006, 6 specimens, 65.0–166.0 mm SL, the Tongtian River, Zhiduo County, Qinghai Province; NWIPB2306007–NWIPB2306016, 10 specimens, the Dangqu River, 58.0–152.0 mm SL, Zaduo County, Qinghai Province; NWIPB2306017–NWIPB2306029, 13 specimens, 54.0–161.0 mm SL, the Chumar River, Qumalai County, Qinghai Province.

Schizopygopsis chengi: NWIPB2107011 and NWIPB2107012, two specimens, 108.0–164.0 mm SL, the Marke River, Banma County, Qinghai Province.

Schizopygopsis pylzovi: NWIPB1205412–5, four specimens, 146.2–157.3 mm SL, the Yellow River, Gande County, Qinghai Province.

Schizopygopsis kessleri: NWIPB2007004, NWIPB2007006, NWIPB2007051, NWIPB2007054, four specimens, 107.6–128.2 mm SL, the Golmud River, Golmud City, Qinghai Province.

Schizopygopsis kialingensis: NWIPB1108004–007, four specimens, 90.3–95.4 mm SL, the Bailong River, Diebu County, Gansu Province.

Schizopygopsis anteroventris: NWIPB1108432–5, four specimens, 142.3–154.2 mm SL, the Lancang River, Nangqian County, Qinghai Province.

Schizopygopsis stoliczkai: NWIPB1007024 and NWIPB100705, two specimens, 95.0–103.6 mm SL, the Qaraqash River, Pishan County, the Xingjiang Uygur Autonomous Rigon; NWIPB1160487, one specimen, 142.8 mm SL, Pangong Co, Tibet Autonomous Rigon; NWIPB1160383, one specimen, 196.6 mm SL, the Lake Manasarovar, Pulan County, Tibet Autonomous Rigon.

Schizopygopsis thermalis: NWIPB1170189 – NWIPB1170192, four specimens, 98.3–103.4 mm SL, the Yuqu River, Zuogong County, Tibet Autonomous Rigon.

Schizopygopsis younghusbandi: NWIPB1160962–3, two specimens, 87.6–98.2 mm SL, the Pengqu River, Dingri County, Tibet Autonomous Rigon; NWIPB0906028–9, two specimens, 85.3–95.6 mm SL, Nyang River, the Nyingchi City, Tibet Autonomous Rigon.

Molecular analysis

Caudal fins (~ 20 mg) of the samples were cut and homogenized for DNA extraction using an Animal Genomic DNA Purification Kit (Sangon Biotech, China) according to the manufacturer's instructions. After the examination of DNA quality using 1% gel electrophoresis, sequences of the mitochondrial gene cytochrome b (Cyt *b*) were amplified by using the universal primers L14724 (5'–GACTTGAAAAACCACCGTTG–3') and H15915 (5'–CTCCGATCTCCGGATTACAAGAC–3') as described in a previous report (Xiao et al. 2001). PCR was carried out with the following cycling conditions: denaturation at 95 °C for 5 min; 35 cycles of three steps, including a denaturation step at 95 °C for 30 sec, an annealing step at 55 °C for 35 sec, an extension step at 72 °C for 1 min, and a final step at 72 °C for 10 min. The PCR products of the 1140 bp target band were checked by visualization through a 1% low-melting agarose gel and then purified using a DNA Gel Extraction Kit (Sangon Biotech, China). The purified PCR products were sequenced in an ABI 3730 sequencer (Agilent Technologies, USA).

Genetic distance and genetic differentiation

The sequences of Cyt *b* were assembled using the SeqMan program (DNAstar) (Burland 2000), aligned using MAFFT (v7.480) (Katoh et al. 2005), and then trimmed to 1140 bp using MEGA11 (Tamura et al. 2021), which were then deposited in GenBank (Table 2). Additionally, we obtained the Cyt *b* sequences of nine *Schizopygopsis* fishes from GenBank (Du et al. 2016; Li et al. 2016a, b; Zeng et al. 2016; Tian et al. 2025) (Table 2). In total, the Cyt *b* sequences of 62 *Schizopygopsis* fish were used to calculate genetic differentiation (F_{st}) and genetic distance using DnaSP (v 6.12) and MEGA 11 (Rozas et al. 2017; Tamura et al. 2021).

Phylogenetic analysis and molecular species delineation

To infer phylogenetic relationships, the Cyt *b* sequences of *Gymnodiptychus pachycheilus* Herzenstein, 1892, *Oxygymnocypris stewartii* (Lloyd, 1908), *Diptychus maculatus* Steindachner, 1866, *Gymnodiptychus dybowskii* (Kessler, 1874), and *Gymnodiptychus integrigymnatus* Mo, 1989 were retrieved from GenBank as outgroups of *Schizopygopsis* species (Li et al. 2016a, 2016b; Tang et al. 2019) (Table 2). All sequences were imported into PhyloSuite (v1.2.3) for maximum likelihood (ML) and Bayesian inference (BI) analyses (Zhang et al. 2020; Xiang et al. 2023). The best-fit substitution model phylogenetic tree construction was identified using ModelFinder (v2.2.0) based on Bayesian information criterion (BIC), with GTR+F+G4 was selected as the optimal model (Kalyaanamoorthy et al. 2017). The ML tree was constructed using IQ-TREE (v2.2.0), with the support value for each node evaluated via 1,000 bootstrap replications (Nguyen et al. 2015). The BI tree was constructed by two independent runs of 3×10^6 generations with four Markov chain Monte Carlo (MCMC) chain samples every 100 generations with 25% burn-in (Ronquist et al. 2012). Species delimitation was performed by Bayesian implementation of the Poisson tree processes (bPTP) model (https://species.h–its.org/ptp/) (Zhang et al. 2013) and an Assemble Species by Automatic Partitioning (ASAP) model (https://bioinfo.mnhn.fr/abi/

public/asap/asapweb.html) (Puillandre et al. 2021). An unrooted IQ-tree was adopted as a guide tree for bPTP analysis, with the Markov chain Monte Carlo (MCMC) setting as 100,000 generations. The aligned sequence file was selected as input in ASAP, which was run with default parameters, including three substitution models of the p-distances, the Jukes-Cantor (JC69) distances, and the Kimura (K80) TS/TV distances.

Results

Schizopygopsis yalongensis Zhao et al., 2025, sp. nov.

https://zoobank.org/57689429-7B9D-4E37-BCCE-52F4E3097248

Holotype. NWIPB2307001, total length 172.4 mm; standard length 138.7 mm; Western China: Qinghai Province: Chenduo County: Zhenqin Village: Yalong River; 97.60E, 33.38N; Altitude 4,172 m; collected by S. Liu and K. Zhao, July 2023 (Fig. 2).

Paratypes. NWIPB2307002–NWIPB2307041 (40), 65.0–196.0 mm SL, collected with the holotype.

Diagnosis. *Schizopygopsis yalongensis* is distinguished from all other congeners in the genus *Schizopygopsis* by the combination of the following characteristics: the commencement of the ventral fin under the 4th–5th branched ray of the dorsal fin, the outer gill rakers in the first gill arch 15–21, the inner gill rakers in the first gill arch 25–39, the mouth inferior, strong, unbranched rays of dorsal fins with obvious serratures, the pharyngeal bone hooked, tip of the pharyngeal teeth oblique-truncated with the grinding surfaces shovel-shaped.

Schizopygopsis yalongensis is distinguished from *S. malacanthus* by the tip of pharyngeal teeth oblique-truncated with grinding surfaces shovel-shaped (vs. the pharyngeal teeth hooked with the concave grinding surface). *Schizopygopsis yalongensis* is different from *S. thermalis*, *S. younghusbandi*, and *S. kialingensis* by the commencement of the ventral fin under the 4th–5th branched ray of the dorsal fin (vs. the commencement of the ventral fin under the 2nd–3rd branched ray of the dorsal fin). *Schizopygopsis yalongensis* is different from *S. chengi* by having strong unbranched rays of dorsal fins with obvious serratures (vs. weak and soft unbranched rays of dorsal fins with few serratures or no serratures). *Schizopygopsis yalongensis* is different from *S. stoliczkai* by having hooked pharyngeal bone (vs. a wide and triangle-shaped pharyngeal bone). *Schizopygopsis yalongensis* is different from *H. microcephalus* by having two rows of pharyngeal teeth (vs. one row of pharyngeal teeth) (Table 3).

Description. D. iv, 7–8; P. i, 16–19; V. i, 8–10; A. iii, 5; the outer gill rakers in the first gill arch 15–21; the inner gill rakers in the first gill arch 25–39; pharyngeal teeth in 2 rows, 4.3/3.4; vertebrae 4 + 43–45.

The morphometric measurements of the holotype and paratypes are listed in Table 4. Body elongate, somewhat compressed. Dorsal profile arched and sloping, with the greatest depth at the anterior edge of the dorsal fin. Ventral profile less curved. Head conical. Dorsal profile of head convex and sloping. Ventral profile of the head somewhat flat, much so at the mouth region. Snout obtuse and round, length 27.1 (22.9–34.9) % head length. No barbels. Eye round, uplateral in the head. Eye diameter 21.0 (17.1—27.8) % head length. A row of mucous cavities on the chin and cheeks. Nostrils nearer to eye than to tip of snout. Mouth inferior, oral fissure transverse or nearly straightly hooked, the inner side of the lower jaw sharp with a strong horny layer, the length of the lower jaw approximate to the eye diameter. Angle of mouth ending vertically before the anterior of eye. Lower lip narrow with two lateral lobes, posterior groove of the lower lip discontinued. Body nearly scaleless, except 1–4 rows of minute scales on the pectoral girdle and a sheath consisting of 16–20 scales at base of anal fin behind ventral fin. Lateral line complete, along middle of flank and caudal peduncle, the anterior portion skinfold-like. The last unbranched dorsal fin ray strong with obvious serratures at the posterior edge. The origin of the dorsal fin approximate in the middle point between the tip of the snout and the base of the caudal fin, anterior dorsal angle of fin squarish with roundish corner. Ray of dorsal fin slender. Commencement of the ventral fin under the 4–5th branched ray of the dorsal fin. The anterior end of anal scaly sheath exceeding the middle point between the ventral and anal fins. Anal opening near origin of anal fin. Posterior border of anal fin somewhat obliquely truncated and the lower posterior angle prolonged and roundish at tip, tip reaching lower base of caudal fin. Caudal fin deeply forked. Gill rakers small, short with pointed tips, moderately dense set. Pharyngeal bone hooked. Pharyngeal teeth in 2 rows, shovel-shaped or oblique-truncated tip.

Color pattern. For the alcohol-preserved specimens; back gray, abdomen yellowish to grayish white, back, head, and dorsal fin with blackish gray spots.

For life colour (Fig. 3); back and head yellowish brown, abdomen white, lateral line white, back, head, and dorsal fin with blackish grey spots. Dorsal, caudal, anal, pelvic, and pectoral fins pale brown.

Ecology. *Schizopygopsis yalongensis* is distributed exclusively in the upstream of the Yalong River in Chenduo County, Qinghai Province, China. *Schizopygopsis yalongensis* inhabits cold streams in the upstream of the Yalong River, with the riverbed consisting of sands, gravel, and pebbles at altitudes greater than 3,000 m (Fig. 4). The coexisting fish include *Gymnodiptychus pachycheilus* Herzenstein, 1892, *Triplophysa stoliczkae* (Steindachner, 1866), *Triplophysa leptosoma* (Herzenstein, 1888), and *Triplophysa orientalis* (Herzenstein, 1888).

Etymology. The name of the new species, *yalongensis*, is derived from the Yalong River (雅砻江), where the species dwells. The Chinese name for the species is suggested as 雅砻裸裂尻鱼 (*Schizopygopsis yalongensis*).

Genetic and phylogenetic analyses. In total, sequencing of Cyt *b* from 75 specimens generated 46 haplotypes, including 18 from *S. yalongensis*, 24 from *H. microcephalus*, and 4 from *S. malacanthus*. Together with

Figure 2. Holotype of *S. yalongensis*. **a.** Lateral view of *S. yalongensis*; **b.** Dorsal view of *S. yalongensis*; **c.** Ventral view of *S. yalongensis*; **d.** Lateral view of *S. yalongensis* via micro-CT scanning; **e.** The inside of the gill arch from the left side of *S. yalongensis*; **f.** The outside of the gill arch from the left side of *S. yalongensis*; **g.** Pharyngeal teeth of *S. yalongensis*.

16 sequences of Cyt *b* from 7 *Schizopygopsis* fishes from GenBank (Table 2), genetic distances among all *Schizopygopsis* fishes were calculated, which ranged from 0.132% (between *Schizopygopsis kessleri* and *Schizopygopsis pylzovi*) to 7.149% (between *Schizopygopsis anteroventris* and *Schizopygopsis chengi*). The genetic distance was 2.03–6.16% between *S. yalongensis* and other fish in the genus *Schizopygopsis*, with an average distance of 4.15%. The genetic distance between *S. yalongensis* and *S. malacanthus* was 3.605%, which was greater than that between *S. kessleri* and *S. pylzovi*, *S. kessleri* and *Schizopygopsis kialingensis*, *S. kessleri* and *H. microcephalus*,

Table 3. Morphological characters in the genus *Schizopygopsis*.

Species	The commencement of ventral fin	Unbranched dorsal fin ray	Mouth	Horny layer of lower jaw	Fin ray	ING/ONG	Anal scales	Pharyngeal teeth
S. yalongensis	under the 4–5th branched ray of dorsal fin	Strong with obvious serratures	Inferior, transverse or slightly hooked	Wide, straight and sharp	D vi, 8; P i, 17–19 V i, 8–9; A iii, 5	29–33/15–18	reaching the base of ventral fin	Two rows, tip oblique–truncated, grinding surfaces shovel–shaped
S. stoliczkai	under the 4–5th branched ray of dorsal fin	Strong with obvious serratures	Inferior, transverse or slightly hooked	Wide, straight and sharp	D vi, 8; P i, 17–19 V i, 8–9; A iii, 5	29–33/15–18	reaching the base of ventral fin	Two rows, tip oblique–truncated
S. chengi	under the 4–5th branched ray of dorsal fin	Soft with few and tiny serratures	Inferior, straightly transverse	Wide, straight and sharp	D vi, 8; P i, 19–21 V i, 9; A iii, 5	25–37/15–20	reaching the base of ventral fin	Two rows, tip hooked, pharyngeal teeth columnar, grinding surface concave
S. malacanthus	under the 4–5th branched ray of dorsal fin	Strong with serratures	Inferior, transverse or slightly hooked	Wide, straight and sharp	D vi, 8; P i, 16–18 V i, 8–10; A iii, 5	26–38/16–25	reaching the midpoint between ventral and anal fins	Two rows, tip hooked with the concave grinding surface
S. kessleri	under the 2–3th branched ray of dorsal fin	weak with tiny serratures	Inferior, transverse or slightly hooked	Sharp and narrow	D vi, 8; P i, 17–19 V i, 8–9; A iii, 5	27–31/16–18	reaching the base of ventral fin	Two rows, tip hooked, grinding surface concave
S. pylzovi	under the 2–3th branched ray of dorsal fin	Strong with obvious serratures	Inferior, transverse and big	Sharp and narrow	D vi, 8; P i, 15–17 V i, 8–9; A iii, 5	29–31/16–18	reaching the base of ventral fin	Two rows, tip hooked, grinding surface concave
S. thermalis	under the 4–5th branched ray of dorsal fin	Strong with obvious serratures	Inferior or sub-inferior	Thin and sharp	D vi, 8; P i, 19 V i, 9; A iii, 5	19–20/11–12	reaching the midpoint between ventral and anal fins	Two rows, grinding surface shovel–shaped
S. younghusbandi	under the 4–5th branched ray of dorsal fin	weak and smooth	Inferior, transverse or hooked	Sharp and narrow	D vi, 8; P i, 18–19 V i, 8–9; A iii, 5	19–20/11–12	reaching the base of ventral fin	Two rows, tip hooked, grinding surfaces shovel–shaped
S. kialingensis	under the 2–3th branched ray of dorsal fin	weak and smooth	Inferior or sub-inferior, deeply hooked	Thin and sharp	D vi, 8; P i, 17–19 V i, 8–9; A iii, 5	14–16/10–12	reaching the base of ventral fin or midpoint between ventral and anal fins	Two rows, tip hooked, grinding surface concave
S. anteroventris	under the 1st branched ray of dorsal fin	Strong with obvious serratures	Inferior, transverse or hooked	Sharp	D vi, 7; P i, 17–18 V i, 8–9; A iii, 5	13–15/20–23	reaching the base of ventral fin	Two rows, tip hooked, pharyngeal teeth columnar, grinding surface shovel–shaped
H. microcephalus	under the 3–5th branched ray of dorsal fin	Strong with obvious serratures	Inferior or sub-inferior, transverse or deeply hooked	Sharp and narrow	D vi, 8; P i, 17–19 V i, 8; A iii, 5	15–25/25–38	reaching the base of ventral fin	one row, tip oblique–truncated, pharyngeal teeth thin and round

S. kialingensis and *S. pylzovi*, *H. microcephalus* and *S. pylzovi*, and *S. malacanthus* and *S. thermalis* (Table 4). The genetic differentiation (F_{st}) ranged from 0.0001 (between *S. kessleri* and *S. pylzovi*) to 0.9950 (between *Schizopygopsis stoliczkai* and *S. younghusbandi*). The F_{st} reached 0.5276 between *S. yalongensis* and *S. malacanthus*, which was greater than those of *S. kessleri–H. microcephalus* and *S. kessleri–S. pylzovi* (Table 5).

The phylogenetic trees were constructed on the basis of 46 haplotypes from *S. yalongensis*, *H. microcephalus*, and *S. malacanthus*, 16 haplotypes from 7 *Schizopygopsis* fishes, and 5 haplotypes from *G. pachycheilus*, *O. stewartii*, *D. maculatus*, *G. dybowskii* and *G. integrigymnatus*. BI and ML trees generated identical topologies, revealing that *S. yalongensis* did not form the closest genetic relationship with *S. malacanthus* (Fig. 5a). The monophyletic *S. yalongensis* was grouped with *S. kialingensis* and then clustered with *S. kessleri*, *S. pylzovi*, and *H. microcephalus*, with strong support (Fig. 5a). According to the ML tree, the bPTP method defined

Figure 3. Live specimen of *S. yalongensis* collected from the Yalong River in Zhenqin Village, Qinghai Province, China. Photograph by Dr. Sijia Liu.

Figure 4. The habitat of the Yalong River where *S. yalongensis* is found.

16 species with Bayesian support values ranging from 0.44 to 1.00, which strongly supported *S. yalongensis* as an independent species, with a Bayesian support value of 0.84 (Fig. 5b). ASAP identified the 5 best partitions based on the pairwise genetic distance. According to the lowest score of 3.5, all the samples were split into 16

Table 4. Morphometric measurements of *S. yalongensis*, *S. malacanthus* and *H. microcephalus*.

Characters	*S. yalongensis* (n=41)			*S. malacanthus* (n=20)		*H. microcephalus* (n=29)	
	Holotype	Mean±SD	Range	Mean±SD	Range	Mean±SD	Range
L_t (mm)	172.4	156.5±34.4	80.0–246.0	166.9±5.6	89.0–309.0	130.0±44.6	67.0–198.0
L_s (mm)	138.7	125.9±28.6	65.0–196.0	133.4±4.7	69.0–252	105.1±38.1	54.0–166.0
% of L_s							
BH	19.6	19.5±1.8	14.8–24.6	20.3±1.5	16.9–22.5	17.5±1.8	12.7–21.1
HL	26.1	25.8±1.8	17.5–29.1	22.5±2.0	18.4–28.5	22.8±1.8	19.8–25.3
CPL	13.0	13.4±1.7	9.9–16.9	13.2±1.5	11.1–17.9	13.3±1.5	9.9–16.2
CPD	8.1	7.8±0.5	7.0–9.0	8.7±0.5	7.7–9.5	7.1±0.8	5.9–9.0
PDL	48.2	47.4±2.0	43.1–51.1	46.4±2.0	42.4–51.0	48.7±1.9	45.1–53.2
PPL	26.3	26.4±1.3	23.2–28.9	23.0±1.6	20.2–25.8	24.6±2.0	21.3–28.5
PEL	54.5	54.3±2.8	45.7–58.8	55.0±1.9	52.5–57.8	56.0±2.9	51.1–68.3
PAL	78.4	77.0±3.6	62.9–83.0	78.0±1.7	74.6–80.6	79.4±2.4	76.5–86.6
% of HL							
HD	66.3	64.9±6.5	59.4–100.0	69.4±5.0	53.3–76.4	62.6±3.3	57.7–70.0
HW	64.1	62.7±6.8	50.0–92.1	64.1±8.0	49.8–80.4	59.3±4.4	52.5–70.0
ED	21.5	21.0±2.2	17.1–27.8	19.8±2.7	15.4–26.3	22.9±3.7	18.2–30.0
IEW	32.2	31.1±3.7	23.2–48.5	35.8±4.4	24.6–42.4	28.6±2.1	25.3–32.9
SL	27.9	27.1±2.5	22.9–34.9	27.7±2.8	19.3–31.8	25.3±2.6	21.4–30.0
MW	35.3	34.7±4.4	26.0–54.4	37.0±5.6	27.1–47.5	30.2±2.8	25.1–36.5
PL	54.5	53.1±4.8	47.5–76.8	51.7±3.5	40.0–58.1	51.7±3.4	44.9–57.3
Ratio (%)							
CPD/CPL	62.31	59.3±10.3	44.7–89.5	66.7±8.5	45.0–81.3	54.8±8.5	38.2–68.7
MW/SL	126.52	130.9±15.2	102.2–160.0	133.6±14.5	109.5–156.4	122.5±10.1	108.2–142.0
IEW/ED	149.77	149.6±22.6	89.4–207.5	185.0±39.2	120.5–275.9	128.4±22.6	97.5–180.0
Count							
ONG	19	18.24±1.68	15–21	14.2±2.17	12–17	18.67±2.19	14–22
ING	32	31.35±3.18	25–39	24.2±1.30	23–26	29.08±1.83	26–31

SD: standard deviation; Range: including the measurements from holotype.

Table 5. K2P genetic distance (%, lower left diagonal) and genetic differentiation (*F*st, upper right diagonal).

	S yalongensis	*S. malacanthus*	*S. kialingensis*	*S. chengi*	*H. microcephalus*	*S. pylzovi*	*S. kessleri*	*S. stoliczkai*	*S. anteroventris*	*S. thermalis*	*S. younghusbandi*
S. yalongensis		0.5276	0.4035	0.9594	0.7925	0.8549	0.9167	0.9686	0.8645	0.8635	0.9605
S. malacanthus	3.605		0.3650	0.8321	0.6088	0.6531	0.9646	0.7977	0.8693	0.7116	0.7420
S. kialingensis	2.034	3.879		0.8312	0.4434	0.4490	0.4928	0.8125	0.7159	0.7533	0.7722
S. chengi	6.160	6.725	6.75		0.9346	0.9650	0.9620	0.9868	0.9011	0.9809	0.9686
H. microcephalus	2.857	4.449	3.014	6.524		0.7567	0.9083	0.9413	0.8739	0.9206	0.9329
S. pylzovi	2.027	3.933	2.149	6.272	2.405		0.0001	0.9725	0.8738	0.9551	0.9677
S. kessleri	1.901	3.889	2.047	6.316	2.365	0.132		0.9908	0.9039	0.9886	0.9892
S. stoliczkai	5.156	4.971	5.614	6.667	5.786	4.781	4.825		0.8958	0.9897	0.9950
S. anteroventris	4.405	4.503	5.175	7.149	5.280	4.518	4.561	4.561		0.8889	0.9039
S. thermalis	3.928	3.611	3.879	6.886	4.985	3.904	3.947	4.254	4.430		0.8889
S. younghusbandi	4.103	3.918	3.918	6.667	5.161	4.079	4.123	4.386	4.561	3.95	

species, and the samples of *S. yalongensis* were grouped together, with clear separation from *H. microcephalus* and *S. malacanthus* (Fig. 5b). The species delimitation indicated that *S. yalongensis* has an independent taxonomic status with coexisting species.

Morphological analysis. The measurements of 17 morphological characteristics were applied for PCA, which revealed that 56.6% of the total variance was explained by the first two components, with 35.16% explained by PC1 and 21.44% explained by PC2. The results

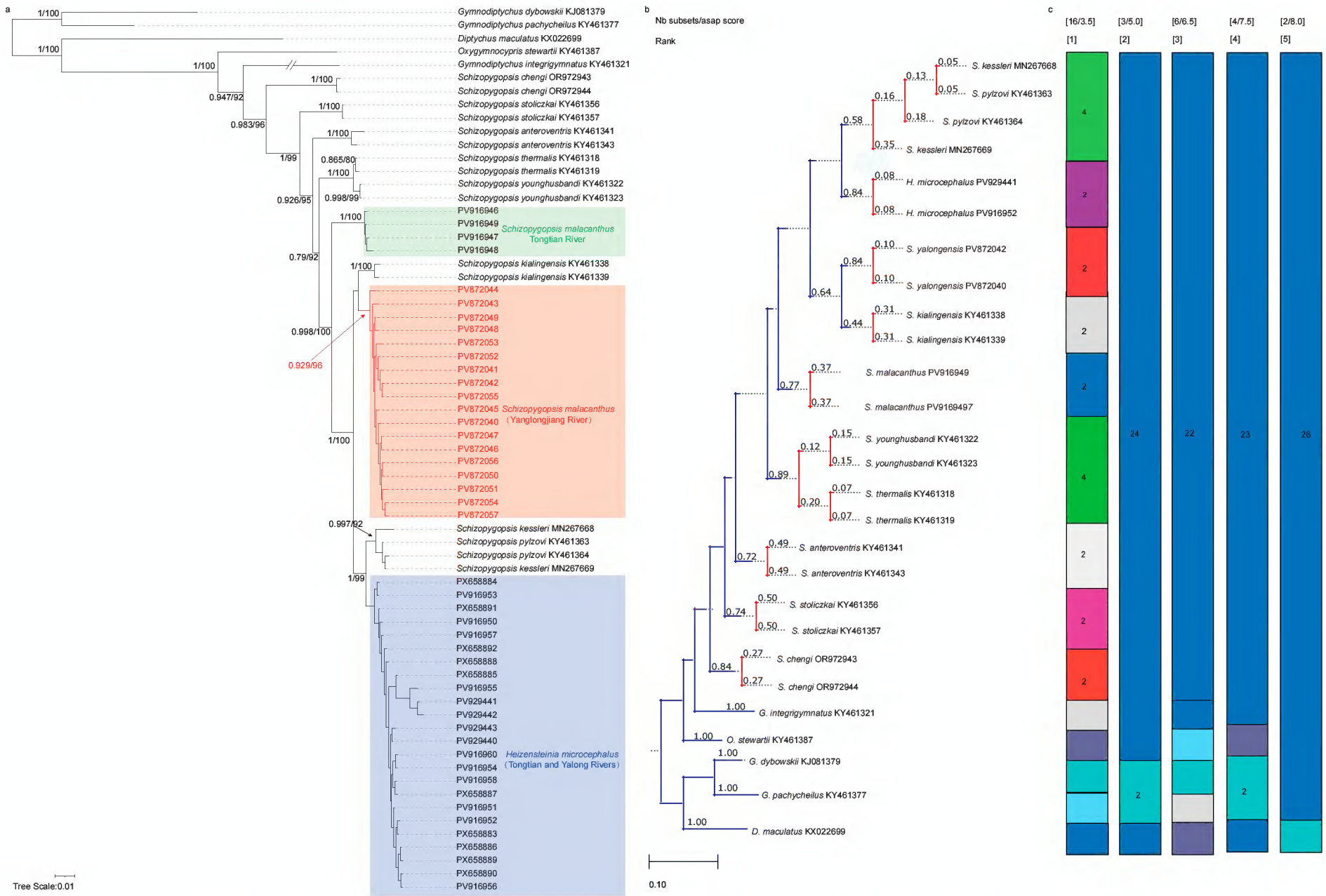

Figure 5. Phylogenetics of the genus *Schizopygopsis*. **a.** ML and BI trees were constructed based on the sequences of Cyt *b*, which demonstrated the same topology. The posterior probabilities and Bayesian support values are labelled on the branches. The red and green squares indicate specimens from *S. yalongensis* and *S. malacanthus*, respectively; **b.** Branches in blue were defined as valid species by bPTP analysis, and branches in red were considered invalid species by bPTP analysis. The posterior probabilities were labelled on branches, indicating the speciation probabilities; **c.** Squares in colors indicate samples for ASAP analysis. The ASAP scores, the number of subsets, and the corresponding ranks for the number of species are listed at the top. A square with the same color is defined as a species. The top 5 partition results are listed.

of the PCA demonstrated that specimens of *S. yalongensis* and *S. malacanthus* were mixed and could not be distinguished from each other (Fig. 6a). Compared with those of *S. yalongensis*, the inner and outer gill rakers of *S. malacanthus* were sparsely distributed (Fig. 6b, c). Additionally, the tips of the pharyngeal teeth were hooked with a concave grinding surface in *S. malacanthus* (Fig. 6d). The morphological differences in the feeding apparatus between *S. yalongensis* and *S. malacanthus* might be related to the distinct eco-environments of the Yalong and Tongtian Rivers (Fig. 6e).

Discussion

Previous studies have shown that populations of *S. malacanthus* from the Yalong River and the Jinsha River are morphologically identical, except for differences in the number of gill rakers between the two populations (Wu and Wu 1992). In the present study, we observed more gill rakers in *S. yalongensis*, consistent with the description by Wu and Wu (1992). Additionally, the shapes of the pharyngeal teeth differed between *S. yalongensis* and *S. malacanthus*. Pharyngeal teeth are an important taxonomic characteristic in the Cyprinidae family and the Schizothoracinae subfamily (Zeng and Liu 2011). Based on the shape and number of rows of pharyngeal teeth, the genera *Platypharodon* Herzenstein, 1891 and *Herzensteinia* were defined in the subfamily Schizothoracinae (Chen and Cao 2000). The diverse morphologies of pharyngeal teeth and the number of gill rakers are associated with food partitioning in fish (Wu and Wu 1992; Zeng and Liu 2009; Zeng and Liu 2011; Walleser et al. 2014). For example, grasping teeth with hooked tips is generally found in omnivorous species, which fulfils the demand for the processing of various diets. Shovel-shaped teeth mainly appear in fish that feed on benthic organisms, facilitating the crushing of benthic invertebrates (Zeng and Liu 2009; Zeng and Liu 2011). Moreover, the study revealed the different gut microbial compositions in *S. yalongensis* and *S. malacanthus* at the phylum, class, and generic levels, suggesting potential divergence in food resources (Yang 2022). Therefore, the divergence in feeding-related apparatuses, such as gill rakers and pharyngeal teeth, might be attributed to the adaptation

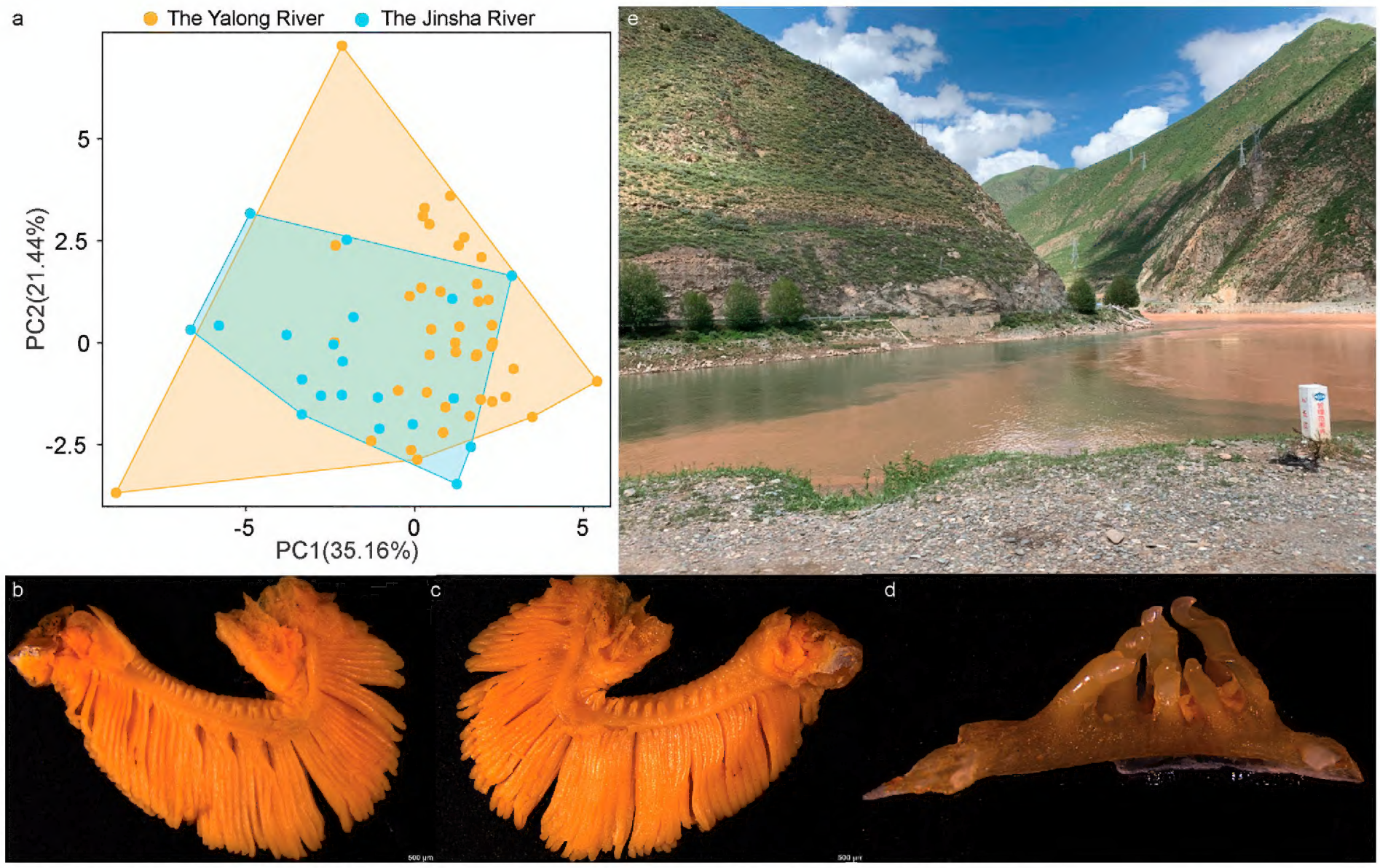

Figure 6. PCA for *S. yalongensis* (orange circles) and *S. malacanthus* (blue circles). **a.** The inside of the gill arch from the left side of *S. yalongensis*; **b.** The outside of the gill arch from the left side of *S. yalongensis*; **c.** The inside of the gill arch from the left side of *S. malacanthus*; **d.** The outside of the gill arch from the left side of *S. malacanthus*; **e.** The habit of *S. malacanthus* in the Tongtian River, which is upstream of the Jinsha River.

of *S. yalongensis* and *S. malacanthus* to different food resources. Therefore, the unique morphology of pharyngeal teeth and gill rakers provides stable characteristics for distinguishing *S. yalongensis* from *S. malacanthus* and other *Schizopygopsis* fishes, possibly because of its unique habits.

Previous studies revealed that the monophyletic groups of *S. malacanthus* in the Yalong and Jinsha Rivers formed a sister relationship, which was presumably due to the absence of other *Schizopygopsis* fishes in the phylogenetic analyses (Li et al. 2020; Wang et al. 2022). Therefore, *S. yalongensis* has long been considered a geographic population or evolutionarily significant unit (ESU) of *S. malacanthus*. By examining all *Schizopygopsis* fish species, the present study revealed the strongly supported monophyly of *S. yalongensis* with phylogenetic proximity to *S. kialingensis* from the Jialing River, a tributary of the Yangtze River. This result was consistent with the genetic distances, genetic differentiation, and species delimitation, confirming the phylogenetic independence of *S. yalongensis* from *S. malacanthus*. The alteration of water systems by the uplift of the QTP in the late Pliocene led to the isolation of the Tongtian and Yalong Rivers (Li 1999; Feng et al. 2023), which impeded gene flow and contributed to the genetic divergence between *S. yalongensis* and *S. malacanthus*. The consistency of this unique morphology and monophyly provide compelling evidence to support the species status of *S. yalongensis*. Additionally, the nested phylogenetic structure of *H. microcephalus* within *Schizopygopsis* fishes challenges the validity of the monotypic genus *Herzensteinia*, which is consistent with previous findings (He and Chen 2007; Qi et al. 2015; Tang et al. 2019).

According to morphological and molecular evidence, we consider *S. yalongensis* a valid species which has important implications for the conservation of the diversity of native fish in the Yalong River. The α diversity of fish is reportedly lower in the Yalong River than in other tributaries of the Jinsha River (Ma et al. 2025). Therefore, the discovery of *S. yalongensis* not only enriches the species diversity of fish but also highlights the possibility of cryptic species of fish in the river systems of the QTP. Additionally, *S. malacanthus* is considered a vulnerable species because of its slow growth, low reproduction rate, and restricted distribution. Considering their similar biological characteristics, *S. yalongensis* is likely a vulnerable species that should receive the same level of protection as *S. malacanthus*.

Key to the species of the genus *Schizopygopsis*

1a Number of gill rakers on the inside of the first gill arch more than 23 ..... 2a
2a Commencement of the ventral fin under the 4–5th branched ray of the dorsal fin 3a
3a Strong unbranched rays of the dorsal fin with obvious serratures 4a
4a Pharyngeal bone wide, triangle 5a
5a Mouth inferior 6a
6a Few gill rakers on the first gill arch, 13–22 (average 17) outer gill rakers, and 23–35 (average 30) inner gill rakes (in river systems in the western QTP) ..... *Schizopygopsis stoliczkai stoliczkai* Steindachner, 1866
6b More gill rakers on the first gill arch, 17–30 (average 21) outer gill rakers, and 29–48 (average 36) inner gill rakers (in Lake Manasarovar) ..... *Schizopygopsis stoliczkai maphamyumensis* Wu & Zhu, 1979
5b Mouth subinferior, oral fissure upwards (in Pangong Tso) ..... *Schizopygopsis stoliczkai bangongensis* Wu & Zhu, 1979
4b Pharyngeal bone hooked 7a
7a Tips of pharyngeal teeth hooked, with the grinding surface concave..... *Schizopygopsis malacanthus* Herzenstein, 1891
7b Pharyngeal teeth shovel shaped or obliquely truncated..... *Schizopygopsis yalongensis* Zhao et al., 2025, sp. nov.
3b The unbranched rays of dorsal fins weak, with few or no serratures 8a
8a Anal scales reaching the base of the ventral fin (in the Marker River and Keke River of the Dadu River Basin) ..... *Schizopygopsis chengi chengi* (Fang), 1936
8b Anal scales reaching the midpoint between the ventral and anal fins 9a
9a Oral fissure hooked, number of outer gill rakers on the first gill arch 10—15, inner gill rakers on the first gill arch 16—23 (in the Baoxing River) ..... *Schizopygopsis chengi baoxingenesis* Fu, Ding & Ye, 1994
9b Oral fissure transverse, number of outer gill rakers on the first gill arch 17–21, inner gill rakers on the first gill arch 25–37 (in the Duoke River) ..... *Schizopygopsis chengi duokeheensis* Tian et al., 2025
2b Commencement of the ventral fin under the 2nd—3rd branched ray of the dorsal fin 10a
10a The last unbranched ray of dorsal fin weak with few tiny serratures, the first outer gill raker outwardly hooked with small serrations (in the Chaidamu River) ..... *Schizopygopsis kessleri* Herzenstein, 1891
10b The last unbranched ray of dorsal fin strong with obvious serratures, the first outer gill raker normal without serrations (in the upper stream of the Yellow River) ..... *Schizopygopsis pylzovi* Kessler, 1876
1b Number of gill rakers on the inner surface of the first gill arch less than 23 ..... 11a
11a Commencement of the ventral fin under the 4–5th branched ray of the dorsal fin 12a
12a The last unbranched ray of dorsal fin strong with obvious serratures (in hot springs in the Tanggula Mountains)..... *Schizopygopsis thermalis* Herzenstein, 1891
12b The last unbranched ray of the dorsal fin weak with few tiny serratures or without serratures 13a
13a A strong horny sheath in the lower lip 14a
14a Commencement of the ventral fin under the 5th branched ray of the dorsal fin, more gill rakers on the first gill arch, with numbers of outer gill rakers 9—14 and inner gill rakers 15–22 (in the Yarlung Zangbo and Pengqu Rivers)..... *Schizopygopsis younghusbandi younghusbandi* Regan, 1905
14b Commencement of the ventral fin under the 4th branched ray of the dorsal fin, fewer gill rakers on the first gill arch, with 8–12 outer gill rakers and 14–22 inner gill rakers (in the Boqu River) ..... *Schizopygopsis younghusbandi himalayensis* Tsao, 1975
13b A weak horny sheath on lower lip, usually with a leather-like, sharp covering at the front edge of the lower lip, with more gill rakers on the first gill arch, with 9—13 outer gill rakers and 18—23 inner gill rakers (in Ngamring Lake).. *Schizopygopsis younghusbandi wui* Tchang, Yueh & Hwang, 1964
11b Commencement of ventral fin under 2nd—3rd branched ray of dorsal fin (in the Jialing River) ..... *Schizopygopsis kialingensis* Tsao & Tun, 1962

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References

Burland TG (2000) DNASTAR's Lasergene sequence analysis software. In: Misener S, Krawetz SA (Eds) Bioinformatics Methods and Protocols: Methods in Molecular Biology 132: 71–91. https://doi.org/10.1385/1-59259-192-2:71

Cao WX, Deng ZL (1962) Schizothoracine fishes of western Sichuan and adjacent regions. Acta Hydrobiogica Sinica 2: 27–53. https://doi.org/10.3724/issn1000-3207-1962-2-27-h

Chen YF, Cao WX (2000) Fauna Sinica, Osteichthyes, Cypriniformes, Schizothoracinae. Beijing Science Publisher, Beijing, 368–384.

Du ZJ, Wu JY, Lin RN, Zhu GX, Xie M, Wang Q, Jiang YZ, Wen AX (2016) Complete mitochondrial genome of *Schizopygopsis chengi* (Cyprinidae, Schizothoracinae, *Schizopygopsis*). Mitochondrial DNA. Part A, DNA Mapping, Sequencing, and Analysis 27: 3717–3718. https://doi.org/10.3109/19401736.2015.1079872

Feng C, Wang K, Xu W, Yang L, Wanghe K, Sun N, Wu B, Wu F, Yang L, Qiu Q, Gan X, Chen Y, He S (2023) Monsoon boosted radiation of the endemic East Asian carps. Science China. Life Sciences 66: 563–578. https://doi.org/10.1007/s11427-022-2141-1

He D, Chen Y (2007) Molecular phylogeny and biogeography of the highly specialized grade schizothoracine fishes (Teleostei: Cyprinidae) inferred from cytochrome b sequences. Chinese Science Bulletin 52: 777–788. https://doi.org/10.1007/s11434-007-0123-2

Kalyaanamoorthy S, Minh BQ, Wong TKF, von Haeseler A, Jermiin LS (2017) ModelFinder: Fast model selection for accurate phylogenetic estimates. Nature Methods 14: 587–589. https://doi.org/10.1038/nmeth.4285

Katoh K, Kuma K, Toh H, Miyata T (2005) MAFFT version 5: Improvement in accuracy of multiple sequence alignment. Nucleic Acids Research 33: 511–518. https://doi.org/10.1093/nar/gki198

Li JJ (1999) Studies of the geomorphological evolution of the Qinghai–Xizang (Tibetan) Plateau and Asian monsoon. Haiyang Dizhi Yu Disiji Dizhi 1: 7–17.

Li G, Peng Z, Zhang R, Tang Y, Tong C, Feng C, Zhang C, Zhao K (2016a) Mito–nuclear phylogeography of the cyprinid fish *Gymnodiptychus dybowskii* in the arid Tien Shan region of Central Asia. Biological Journal of the Linnean Society. Linnean Society of London 118: 304–314. https://doi.org/10.1111/bij.12724

Li G, Tang Y, Zhang R, Zhao K (2016b) Phylogeography of *Diptychus maculatus* (Cyprinidae) endemic to the northern margin of the QTP and Tien Shan region. BMC Evolutionary Biology 16: e186. https://doi.org/10.1186/s12862-016-0756-3

Li X, Yang K, Tong L, Hou F, Liu Q, Li J, Lu Y, Song Z (2020) Phylogeography of *Schizopygopsis malacanthus* Herzenstein (Cypriniformes, Cyprinidae) in relation to the tectonic events and Quaternary climatic oscillations in the Shaluli Mountains Region. Zoology: Analysis of Complex Systems, ZACS 143: e125835. https://doi.org/10.1016/j.zool.2020.125835

Ma W, Liu L, Li K, Jian S, Xue C, Han Q, Wei J, Chen S, Niu Y, Cui Z, Sui R, Tian F, Zhao K (2025) Fish diversity and distribution in the source region of the Yangtze River in Qinghai Province. Shengwu Duoyangxing 33(24494): 1–13. https://doi.org/10.17520/biods.2024494

Nguyen LT, Schmidt HA, von Haeseler A, Minh BQ (2015) IQ–TREE: A fast and effective stochastic algorithm for estimating maximum–likelihood phylogenies. Molecular Biology and Evolution 32: 268–274. https://doi.org/10.1093/molbev/msu300

Nichols JT, Chu YTJC (1935) Comparative studies on the scales and on the pharyngeals and their teeth in chinese cyprinids, with particular reference to taxonomy and evolution. Biology 1935: e198. https://doi.org/10.2307/1436747

Puillandre N, Brouillet S, Achaz G (2021) ASAP: Assemble species by automatic partitioning. Molecular Ecology Resources 21: 609–620. https://doi.org/10.1111/1755-0998.13281

Qi D, Guo S, Chao Y, Kong Q, Li C, Xia M, Xie B, Zhao KJZS (2015) The biogeography and phylogeny of schizothoracine fishes (*Schizopygopsis*) in the Qinghai□Tibetan Plateau. Zoologica Scripta 44: 523–533. https://doi.org/10.1111/zsc.12116

Ronquist F, Teslenko M, van der Mark P, Ayres DL, Darling A, Hohna S, Larget B, Liu L, Suchard MA, Huelsenbeck JP (2012) MrBayes 3.2: Efficient bayesian phylogenetic inference and model choice across a large model space. Systematic Biology 61: 539–542. https://doi.org/10.1093/sysbio/sys029

Rozas J, Ferrer–Mata A, Sanchez–DelBarrio JC, Guirao–Rico S, Librado P, Ramos–Onsins SE, Sanchez–Gracia A (2017) DnaSP 6: DNA sequence polymorphism analysis of large data sets. Molecular Biology and Evolution 34: 3299–3302. https://doi.org/10.1093/molbev/msx248

Tamura K, Stecher G, Kumar S (2021) MEGA11: Molecular Evolutionary Genetics Analysis Version 11. Molecular Biology and Evolution 38: 3022–3027. https://doi.org/10.1093/molbev/msab120

Tang Y, Li C, Wanghe K, Feng C, Tong C, Tian F, Zhao K (2019) Convergent evolution misled taxonomy in schizothoracine fishes (Cypriniformes: Cyprinidae). Molecular Phylogenetics and Evolution 134: 323–337. https://doi.org/10.1016/j.ympev.2019.01.008

Tian F, Liu S, Chen S, Zhao K (2025) Revision of *Schizopygopsis chengi* Fang 1936 (Cypriniformes: Cyprinidae), with a description of a new subspecies. Zootaxa 5590: 481–506. https://doi.org/10.11646/zootaxa.5590.4.2

Walleser LR, Sandheinrich MB, Howard DR, Gaikowski MP, Amberg JJ (2014) Spatial and temporal variation of the gill rakers of gizzard shad and silver carp in three Midwestern Rivers. North American Journal of Fisheries Management 34: 875–884. https://doi.org/10.1080/02755947.2014.920740

Wang X, Tong L, Deng J, Li L, Xiang P, Xu L, Luo Z, Yang K, Song Z (2022) Insights into historical drainage evolution based on the phylogeography of *Schizopygopsis malacanthus* Herzenstein (Cypriniformes, Cyprinidae) across the upper and middle Yalong River drainage in the Hengduan Mountains region, southwest China. Global Ecology and Conservation 35: e02084. https://doi.org/10.1016/j.gecco.2022.e02084

Wu Y, Wu C (1992) The fishes of the Qinghai–Xizang plateau. Chengdu: Sichuan Publishing House of Science and Technology.

Xiang CY, Gao F, Jakovlic I, Lei HP, Hu Y, Zhang H, Zou H, Wang GT, Zhang D (2023) Using PhyloSuite for molecular phylogeny and tree–based analyses. iMeta 2. https://doi.org/10.1002/imt2.87

Xiao W, Zhang Y, Liu H (2001) Molecular systematics of Xenocyprinae (Teleostei: Cyprinidae): taxonomy, biogeography, and coevolution

of a special group restricted in East Asia. Molecular Phylogenetics and Evolution 18: 163–173. https://doi.org/10.1006/mpev.2000.0879

Yang C (2022) Population Genetic Structure and Gut Microbial Diversity of the *Schizopygopsis malacanthus*. Master Thesis, Qinghai University, Xining, China.

Yu CJ, Song ZB, Yue BS (2006) Taxonomic implications from phylogenetic relationships of subspecies of (Pisces: Cyprinidae) based on sequence analysis of cytochrome and mitochondrial DNA control region. Journal of Natural History 40: 2569–2576. https://doi.org/10.1080/00222930601129463

Zeng Y, Liu HZ (2009) Morphological variation of pharyngeal bones and teeth in the subfamily Gobioninae (Cypriniformes: Cyprinidae) and its functional adaptations. Zoological Research 30: 699–706. https://doi.org/10.3724/SP.J.1141.2009.06699

Zeng Y, Liu H (2011) The evolution of pharyngeal bones and teeth in Gobioninae fishes (Teleostei: Cyprinidae) analyzed with phylogenetic comparative methods. Hydrobiologia 664: 183–197. https://doi.org/10.1007/s10750-010-0598-8

Zeng Y, Chen YB, Pan BZ, Zhang DW (2016) Complete mitochondrial genome of *Schizopygopsis chengi baoxingensis* (Teleostei: Cypriniformes: Cyprinidae). Mitochondrial DNA. Part A, DNA Mapping, Sequencing, and Analysis 27: 1405–1406. https://doi.org/10.3109/19401736.2014.982557

Zhang J, Kapli P, Pavlidis P, Stamatakis A (2013) A general species delimitation method with applications to phylogenetic placements. Bioinformatics 29(22): 2869–2876. https://doi.org/10.1093/bioinformatics/btt499

Zhang D, Gao F, Jakovlic I, Zou H, Zhang J, Li WX, Wang GT (2020) PhyloSuite: An integrated and scalable desktop platform for streamlined molecular sequence data management and evolutionary phylogenetics studies. Molecular Ecology Resources 20: 348–355. https://doi.org/10.1111/1755-0998.13096